Amer. Malac. Bull. **23**: 81-87

Reproductive behavior of the dioecious tidal snail *Cerithidea rhizophorarum* (Gastropoda: Potamididae)*

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Abstract: The dioecious snail *Cerithidea rhizophorarum* (Adams, 1855) is distributed along the coasts of the western Pacific up to the Tohoku district, northern Honshu, Japan. It inhabits reed grasslands and mangrove forests with *Kandelia candel* and *Hibiscus hamabo* trees on a mud flat located at the mouth of Atagogawa River in Kiire. Studies of mating and tree climbing behaviors of the species were conducted at this site from April 2000 to May 2003. Mating behavior was observed in July and August 2002. The time of commencement, termination, and duration were recorded for each copulation. The peak of matings during daytime was seen at 1 to 2, and 5 hours before the lowest tide and during nighttime, between 1 hour before and after lowest tide. However, mating rarely occurred on cloudy days. Climbing behavior was observed in an area of 100 square meters where only *K. candel* trees existed. The number of snails on trees was counted, and daily activity of the snails on trees was monitored in summer and winter, hourly throughout the day. The snails were mainly found on mud from spring to summer but frequently climbed up the tree at particular times during summer. Most individuals were on trees and motionless during winter.

Key words: reproduction, dioecious snail, climbing behavior, gastropod

Molluscs have two types of mating systems: dioecy and hermaphroditism (simultaneous hermaphrodite, protandric hermaphrodite, and protogynous hermaphrodite). These divergent patterns of mating systems are found even in the same taxonomic classes. Bisexual reproduction is common in molluscs, and the pattern of fertilization in most classes is internal, but external fertilization is found in some classes. Hermaphroditic species can be divided into ones that can self-fertilize and ones that cannot. Hence molluscs have many divergences in the reproduction pattern and may be the phylum with the most variable reproductive patterns in the animal kingdom. How could such various reproductive strategies evolve?

There are many reports of mating behavior in hermaphrodites such as Pulmonata and Opisthobranchia, but it is rarely reported in dioecious Prosobranchia. A clearer understanding of the mating behavior of this group would be one of the keys to solve the evolution of various reproductive strategies in molluscs.

The dioecious prosobranch snail *Cerithidea rhizophorarum* (Adams, 1855) commonly inhabits tidal flats in eastern Asia. In the tidal flat of the Atagogawa River, Kiire-Cho, Kagoshima, mating by shell mounting was observed (Ohtaki *et al.* 2001). Ohtaki *et al.* (2001) also reported mating behavior, but it was incomplete. In this study, several aspects of mating behavior of *C. rhizophorarum* were examined in the field including duration of copulation both in daytime and nighttime.

MATERIALS AND METHODS

Study site

The tidal flat is at the mouth of Atagogawa River flowing through Kiire-Cho, Kagoshima-city. This river is located by the Nisseki oil camp, and it joins Yahata River in this point. A small mangrove forest consisting of *Kandelia candel* and *Hibiscus hamabo*, at the northern limit of mangrove distribution in the West Pacific, covers this tidal flat. Some species of gastropod, such as *Cerithideopsilla djadjariensis* (K. Martin, 1899), *Cerithideopsilla cingulata* (Gmelin, 1791), *Batillaria multiformis* (Lischke, 1869), *Batillaria cumingi* (Crosse, 1862), *Clypeomorus coralium* (Kiener, 1834), *Reticunassa festiva* (Powy, 1833), *Clithon oualaniensis* (Lesson, 1831), and *Clithon faba* (Sowerby, 1836) inhabit the tidal flat. We established three study sites (A, B, C) 60 m from the shore of Atagogawa River.

Size distribution

We collected 100 *Cerithidea rhizophorarum* with a net (1 mm mesh) at random at the three stations (A, B, C) and

* From the symposium "Gastropod Mating Systems" presented at the joint meeting of the American Malacological Society and Western Society of Malacologists, held 26-30 June 2005 at Asilomar, Pacific Grove, California.

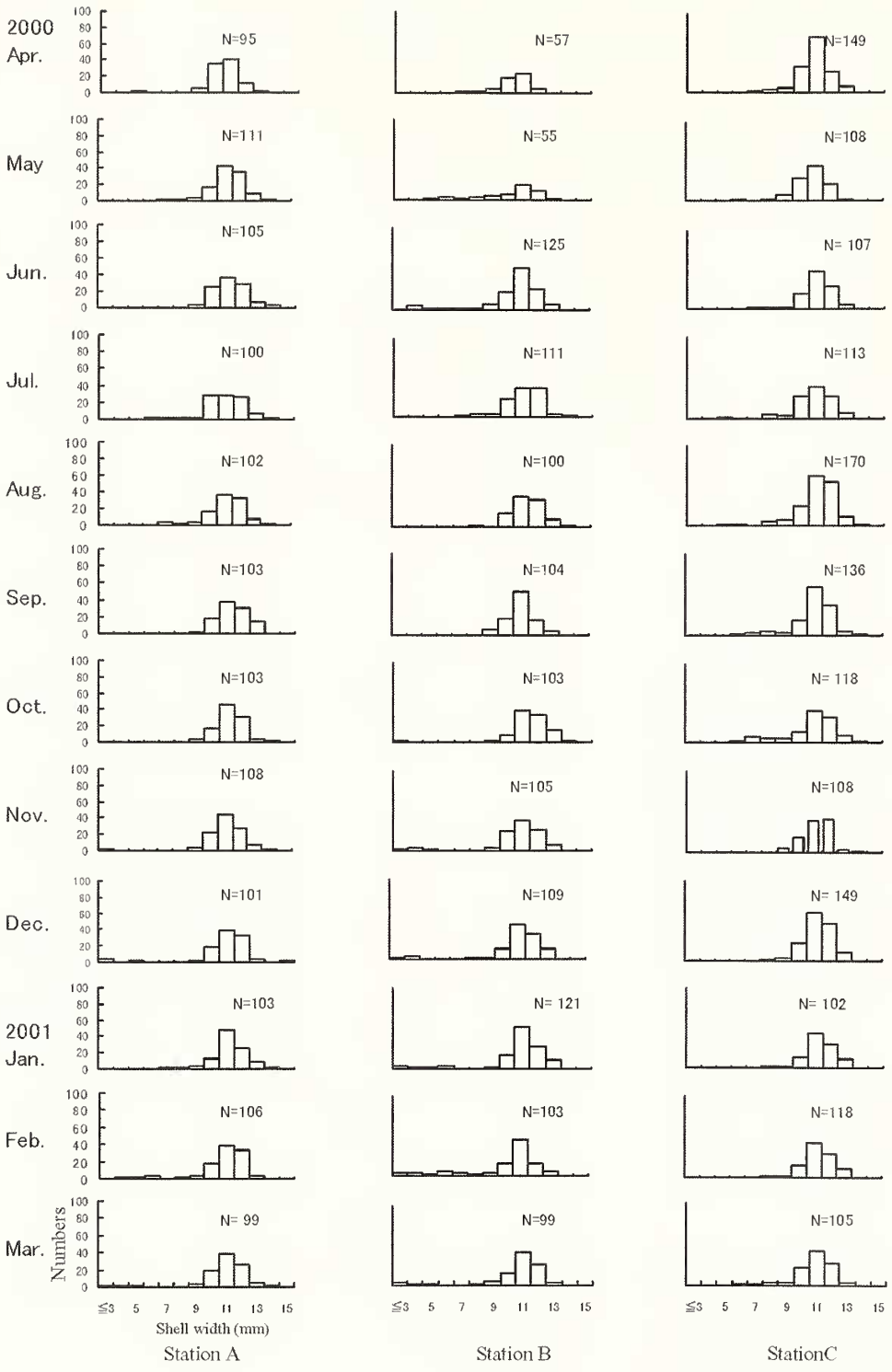
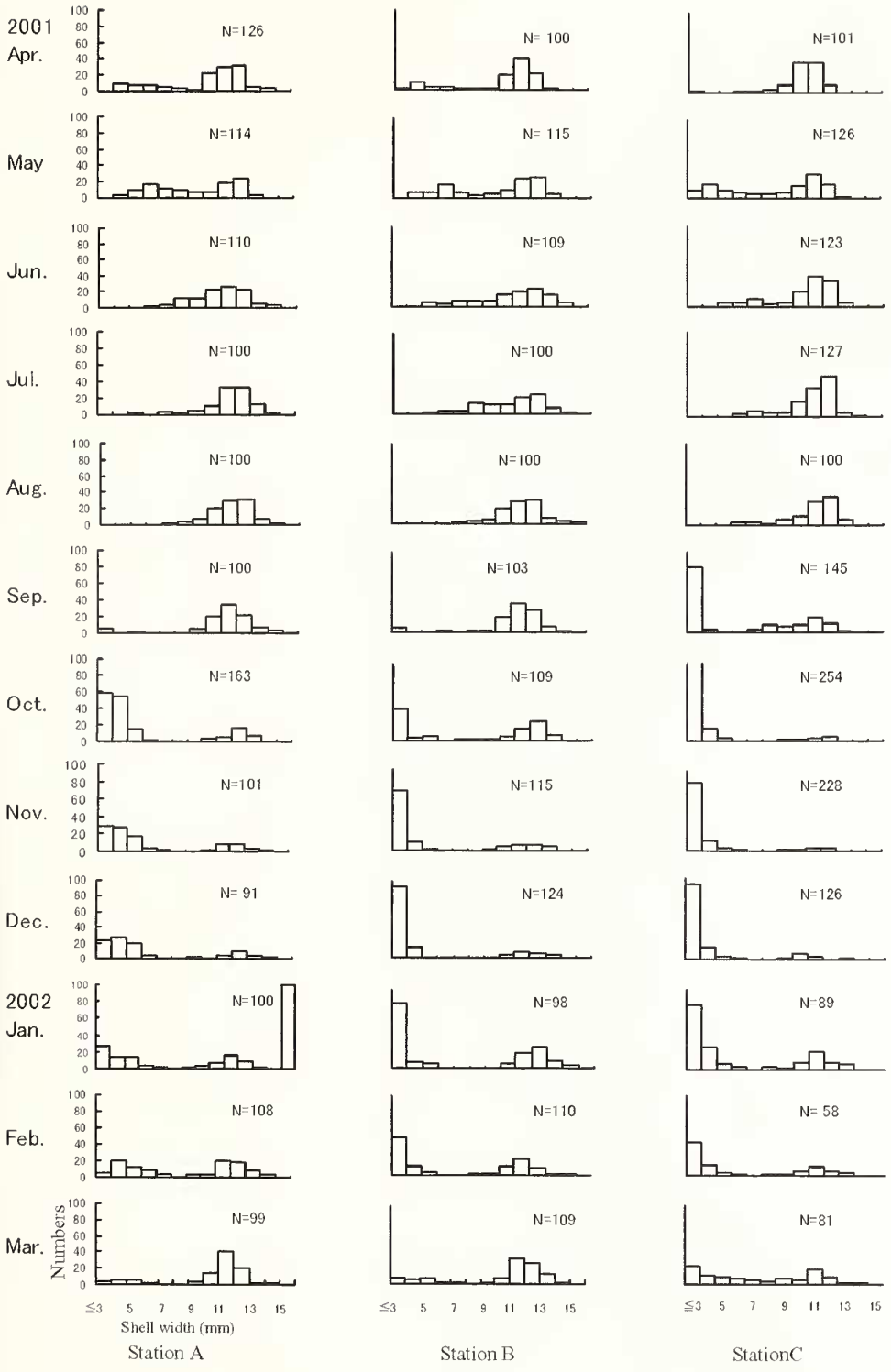


Figure 1. Seasonal change at each station in the width-frequency distribution in *Cerithidea rhizophorarum*.



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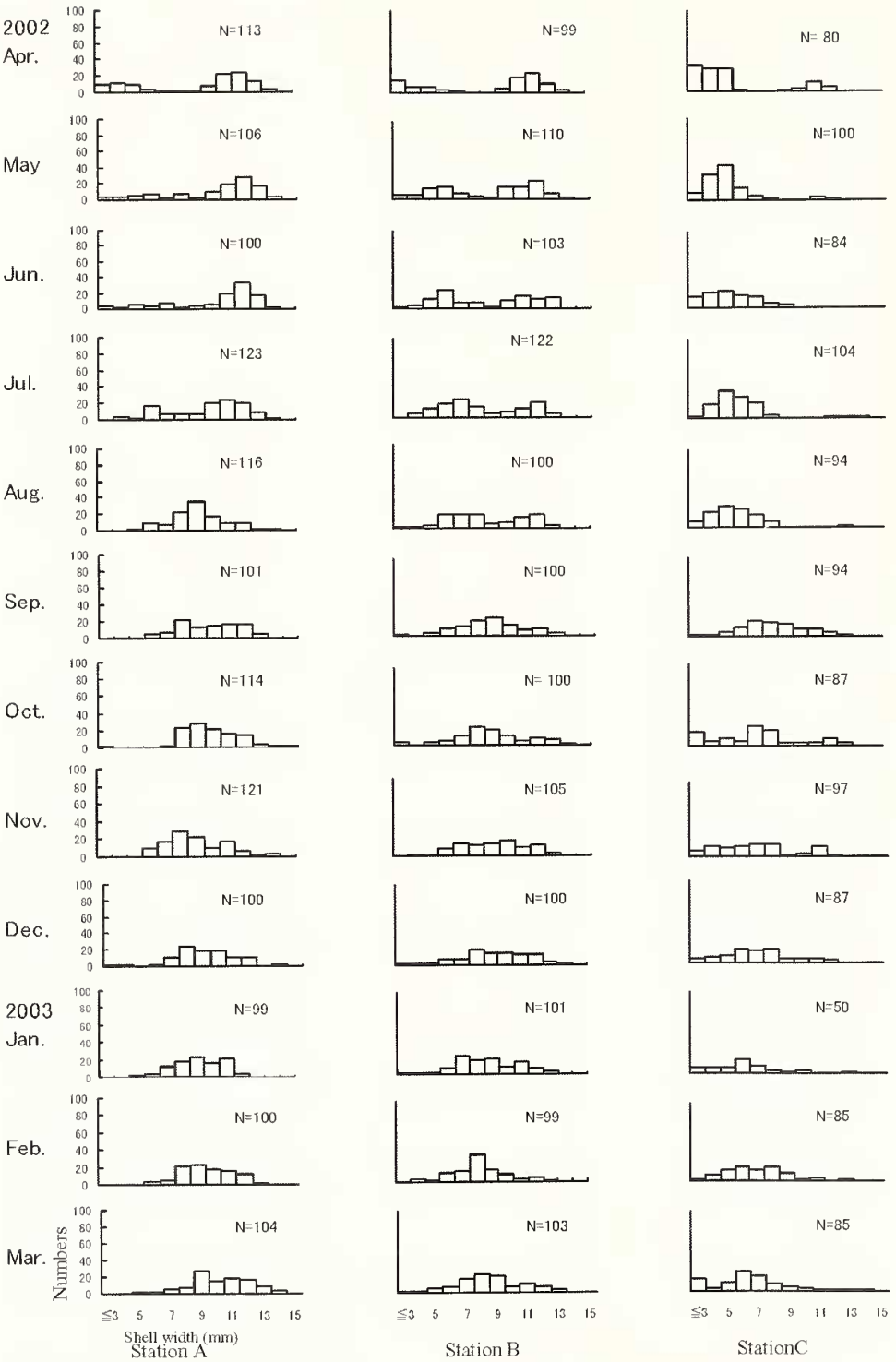

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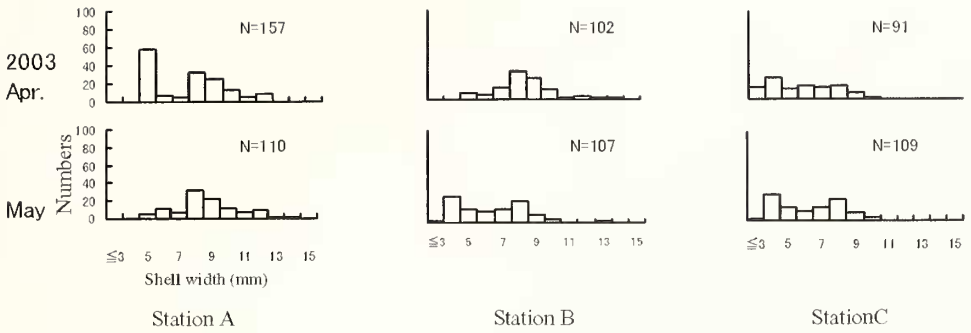

Figure 1. (continued)

measured their shell width *in situ* every month from April 2000 through May 2003.

1. Copulation frequency

Snail mating can be categorized as face-to-face mating or shell-mounting mating (Asami 1998). *Cerithidea rhizophorarum* mates by shell mounting (Ohtaki *et al.* 2001). Ohtaki *et al.* (2001) reported that copulatory behavior was observed from the middle of June to the middle of August and peak of initial time of copulation was before lowest tide. In this study, we counted the number of individuals and copulating couples along the route every 15 minutes on 4 July and 21 July 2001, 12 and 25 June, 12 and 13 July, and 10 August 2002 in daytime, and 12 and 13 July 2002 at night. While sampling the transect every 15 minutes, we placed little flags marked with an identification number near each pair of *C. rhizophorarum* in the act of coupling. When the pair of *C. rhizophorarum* separated, it was assumed that the copulation was terminated. The length between the beginning and the end of the copulation was checked and noted. We used a headlamp for night searches. On the same day, we picked 100 copulation pairs at random and marked upper snails with a permanent marker. We brought copulating pairs back to laboratory and measured them (both weight and shell height). Their shells were broken, and we determined their sex by examining the reproductive gland.

2. Climbing behavior

Cerithidea rhizophorarum is known as an intertidal snail species, but it does climb trees. This behavior was observed in a small mangrove forest of the Atagogawa River (Wakamatu and Tomiyama 2000, Ohtaki *et al.* 2002). In this study, we observed snails on the trees from May 2000 to May 2003, 2 hours after the lowest tide of spring tides every month.

RESULTS

Size distribution

During this period no large change in the number of *Cerithidea rhizophorarum* was noticed (Fig. 1). Newly recruited juveniles (3-6 mm in shell width) of *C. rhizophorarum* were found in higher tidal zones than the other potamidid and batillariid species. The distribution of juveniles of *C. rhizophorarum* was limited to lower tidal zones.

Copulation frequency

The largest number of copulations was observed between one and two hours before the lowest tide in the afternoon and two hours before and after the lowest tide at night (Fig. 2). The mean shell width of upper individuals was 10.96 ± 2.36 mm (mean ± *SD*, $N = 100$, range = 8.6-13.0 mm) and 11.72 ± 29 mm (mean ± *SD*, $N = 100$, range = 8.8-13.9 mm) for lower individuals (Fig. 3). There was no significant correlation between the shell width of upper and lower individuals ($R^2 = 0.082$), but upper individuals were significantly smaller than lower ones (Student's *t*-test, $P < 0.05$). From the reproductive organs of the 100 pairs, 65% were male (upper) - female (lower) pairs, 31% were male - male pairs, 1% female - female pair, and 3% female (upper) - male (lower) pairs were observed. The mean width of individuals with male reproductive organs was 11.49 ± 2.69 mm (mean ± *SD*; $N = 69$, range = 8.8-13.9 mm). There was no relation in shell width between the females and the males (*F*-test; $P \geq 0.05$).

Climbing behavior

There were clear seasonal changes in total number of individuals of *Cerithidea rhizophorarum* on the trunk of the mangrove tree *Kandelia candel* (Fig. 4). In 2000, 1071 snails were observed on trees in May, 1355 in June, 601 in July, 46 snails in August, and in September the number of snails increased to 1041. The following year, from September to December, the number of snails climbing up the trunk of mangrove trees was at its peak, with the number decreasing from February through March. This tendency was seen every year at the same period.

DISCUSSION

Wakamatsu and Tomiyama (2000) reported that recruitment of *Cerithidea rhizophorarum* at this site was so

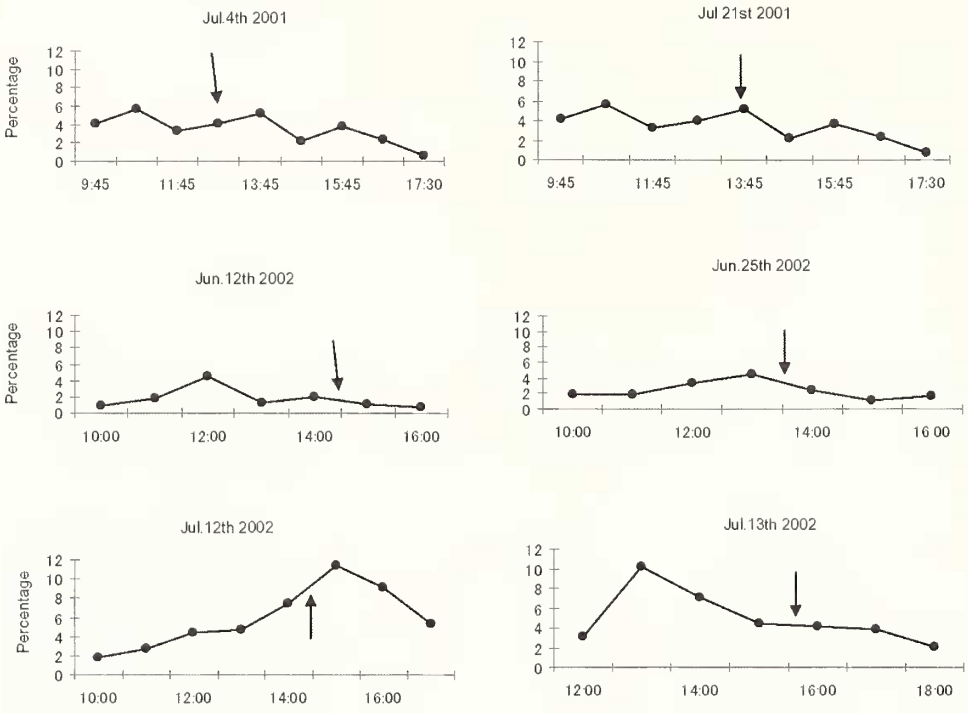

Figure 2. Daily changes in percentage of copulating individuals in the population. Arrows indicate the lowest tides.

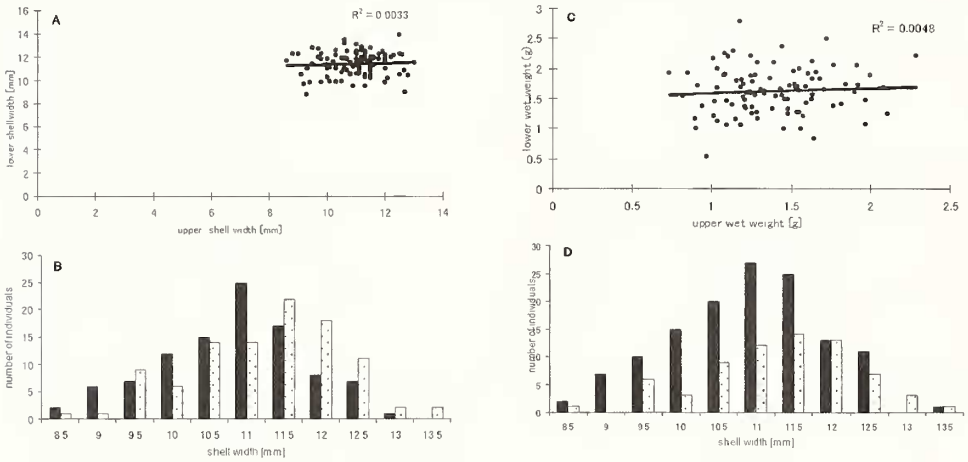

Figure 3. A, Relationship between shell width of upper individuals and lower individuals. $R^2 = 0.0033$, $P > 0.05$, $N = 100$. B, Frequency of shell width of upper individuals and lower individuals. Solid bar, upper individuals; open bar, lower individuals; $N = 100$. C, Relationship between shell width of upper individuals and lower individuals. $R^2 = 0.0048$, $P > 0.05$, $N = 100$. D, Frequency of shell width of male and female. Solid bar, male; open bar, female; $N = 100$.

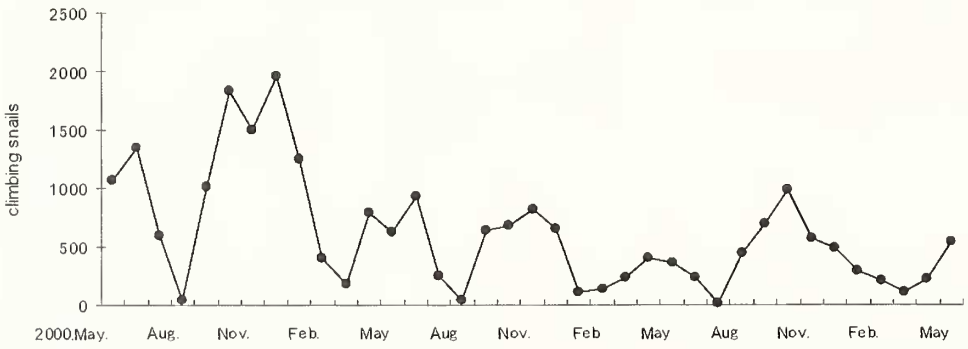

Figure 4. Seasonal changes in total number of individuals of *Cerithidea rhizophorarum* on the trunk of the mangrove tree *Kandelia candel* (May 2000 - May 2003).

small that it could not be detected. But in this study, newly recruited juveniles (3-6 mm) appeared from November 2001 to March 2002, and they grew to 10 mm in length from March to July 2002. However, new recruitment was not observed every year. Wakamatsu and Tomiyama (2000) and Ohtaki *et al.* (2001) suggested that *C. rhizophorarum* had deceased in numbers at this site. We conclude that the decrease in population is due to imposex caused by TBT. From the results of proportions of copulation pairs, it appears males mount females.

More male-to-male (31%) than female-to-female couples were observed (1%), supporting the hypothesis of Wakamatsu and Tomiyama (2000) and Ohtaki *et al.* (2001).

The peak frequency of copulation was generally before the lowest tide in daytime. Copulation was most frequently observed during the 3-6 hours around the time of the lowest tide and mostly during 1-2 hours around the time of the lowest tide at night. As we did not observe copulation when it had begun to rain, rain may block the copulation of *Cerithidea rhizophorarum.*

The population of *Cerithidea rhizophorarum* on trees increased at the highest tide and decreased at the lowest tide. This might be the daily rhythm to avoid the water. Snails were observed on trees from the beginning of spring to June and descended from trees in July to August. These rhythms synchronize with the copulation period. The population on the trees increased in September, and decreased in winter. Climbing trees at the beginning of winter could be in preparation for hibernation.

ACKNOWLEDGEMENTS

We thank Janet Leonard for her help and the invitation to present this study at the symposium, and all participants at the symposium.

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Accepted: 9 May 2007